

## SPATIAL PATTERN AND INTERFERENCE IN PIÑON-JUNIPER WOODLANDS OF NORTHWEST COLORADO

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**ABSTRACT.**—The local spatial arrangement of the coniferous trees *Pinus edulis* and *Juniperus osteosperma* was mapped in two woodland stands and measured in two shrub-dominated stands in the semiarid Piceance Basin of northwest Colorado. In the woodlands, small trees were often clumped, while medium and large trees were either randomly or uniformly dispersed. Significant regressions were obtained between a tree's basal area or canopy area and the area of its Dirichlet domain (the region closer to it than to any other tree). Both findings from the woodland stands accord with results obtained by other workers in other vegetation. Like earlier workers, we interpret these patterns to indicate density-dependent mortality and density-dependent depression of growth rates among the trees in the woodlands. In contrast, the trees in the shrub-dominated stands are located at random with respect to each other. However, they are strongly associated with shrub cover. Apparently, tree seeds arrive in these stands primarily by long-distance dispersal, and the establishment of seedlings is more likely in the shade of shrubs.

Since plants are sessile and their growth is plastic, their arrangement in space and their sizes can reflect the history of their interactions with each other and with the environment. With long-lived, slow-growing plants, studying pattern may be the only feasible way to discover which processes and interactions are important in determining community structure.

We used some of the methods compared by Goodall and West (1979) to study the local spatial arrangement (pattern) of the small coniferous trees *Pinus edulis* and *Juniperus osteosperma* in four stands in the semiarid Piceance Basin of northwest Colorado. Our goals were twofold. First, we wished to determine whether the differences between methods Goodall and West (1979) detected in artificial populations are borne out in more complex real populations. Second, we wished to infer the processes that influence the establishment of seedlings and the growth and mortality of plants.

### STUDY AREA

The Piceance Basin occupies about 3000 km<sup>2</sup> in Garfield and Rio Blanco counties of northwest Colorado. Elevations range from 1707 to 2743 m (Tiedeman and Terwilliger 1978). The climate is semiarid with average

annual precipitation ranging from 28 cm in the northwest to 63.5 cm in the southeast. About half of the annual total falls as snow and most of the remainder as rain in late-summer thunderstorms. In the short term, precipitation is unpredictable and variable (Wymore 1974).

The average annual temperature is 7 C at 1825 m (the elevation of the only permanent weather station in the basin), with a minimum monthly average in January of -5.9 C and a maximum monthly average in July of 20.3 C. The average annual temperature decreases by approximately 0.85 C for every 100 m increase in elevation. Both temperature and precipitation are strongly influenced by local topography (Wymore 1974).

We studied the spatial patterns of *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little (piñon and Utah juniper). Nomenclature follows Goodrich and Neese (1986). *P. edulis* and *J. osteosperma* are small coniferous trees common throughout the western United States, where they form mixed stands, often with an understory of scattered grasses, forbs, and shrubs. They commonly attain heights of 6–8 m, and both reproduce by seed. *P. edulis* usually possesses a single stem, while *J. osteosperma* is often multistemmed.

The vegetation of the basin includes shrublands and woodlands of various floristic

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compositions. Piñon-juniper woodlands (as described in Tiedeman and Terwilliger 1978) have open canopies dominated by *P. edulis* and *J. osteosperma* and occur on broad, flat ridge tops at elevations between 1890 m and 2170 m, where soils are shallow, rocky, light brown, sandy loams (Entisols). Shrublands dominated by *Artemisia tridentata* Nutt. (sagebrush flats) often occur on the same ridges as do piñon-juniper woodlands, at roughly the same elevations, but where soils are finer and deeper. Where piñon-juniper woodlands abut sagebrush flats, zones of intermediate vegetation are often found. In these intermediate areas, the vegetation is dominated by *Artemisia*, with small, scattered individuals of *P. edulis* and *J. osteosperma*. Few of the trees overtop the shrubs.

We studied two piñon-juniper woodlands (stands A and B), which were dominated by mature *P. edulis* and *J. osteosperma*, with little shrub understory. The canopies in these stands are not closed, but individual canopies sometimes abut or overlap. It is known from others (Fowells 1965) and from personal observation that the roots of these trees usually extend beyond the canopy. Thus, neighboring trees which do not seem to be competing for light may nonetheless be competing belowground for water or nutrients. These stands lie at elevations of 2164 m and 1890 m, which approximate the elevational limits of this vegetation in the basin. Stand A slopes  $1.5^\circ$  and faces to the northwest ( $N62^\circ W$ ). Stand B slopes  $3.0^\circ$ , facing to the north-northwest ( $N22^\circ W$ ).

Stands C and D are intermediate between piñon-juniper woodlands and sagebrush flats. None of the trees in these stands is as large as the largest trees in the piñon-juniper woodlands, although many bear cones and are thus sexually mature. These stands occupy ridge tops at elevations of 2164 m and 1981 m. Stand C slopes  $4.5^\circ$ , facing west ( $N80^\circ W$ ), and stand D slopes  $6.5^\circ$ , facing north ( $N5^\circ W$ ).

#### METHODS

Goodall and West (1979) reviewed pattern methods based on analyses of artificial populations. They compared the statistical powers of the methods, that is, the probabilities of rejecting a false null hypothesis. With large samples, all the tested methods gave results

reflecting the true dispersion pattern of artificial populations, with powers approaching 100%. With smaller samples, however, methods differed in power. We used those having the greatest power with small samples: the variance/mean ratio (Clapham 1936) among quadrat methods, and the indices of Hopkins (1954) and Pielou (1959, 1960, 1961) among distance methods (see descriptions below). We also compared the frequencies of quadrats containing exactly 0, 1, 2, . . . plants with the expected Poisson distribution by a chi-squared goodness-of-fit test.

In addition to these methods, we included a measure of pattern that uses information not only about the locations of plants but also about their sizes. The Dirichlet domain (or Thiessen or Voronoi polygon) of a plant comprises all the points closer to that plant than to any other (Honda 1978, Jack 1967, Mead 1971, Mithen, Harper, and Weiner 1984). Its size thus represents the area more easily accessible to the plant than to its neighbors and may represent the amount of resources captured or sequestered by a plant, or potentially more available to it than to its neighbors. This in turn may influence the plant's growth and fitness and indicate what effect, if any, its neighbors have on it. To detect whether this is the case, we regressed the areas of plants' Dirichlet domains on the sizes of the plants.

The variance/mean ratio test (Clapham 1936) is based on the expectation that, in a randomly dispersed population, the frequency distribution of quadrats containing exactly 0, 1, 2, 3, . . . individuals approximates the Poisson distribution. One property of this distribution is that its mean and variance are equal, and their ratio therefore unity. The distribution of this ratio in large samples is approximately normal, with a mean of 1 and a standard deviation of  $(2/n-1)^{1/2}$  (Goodall and West 1979), where  $n$  is the sample size (number of quadrats). In regularly dispersed populations the ratio is less than 1, in aggregated ones greater.

Hopkins's (1954) index  $A$  is based on the expectation that, in a randomly dispersed population, the average distance from randomly located points to the nearest plant equals the average distance between plants and their nearest neighbors. Hopkins proposed the ratio of these two averages as his index:

$$A = (\sum P_i^2) / (\sum I_i^2)$$

where  $P_i$  and  $I_i$  are the sums of equal numbers of distances from random points to the nearest plant and from randomly selected plants to their nearest neighbors, respectively. In a randomly dispersed population, the expected value of  $A$  is 1, and for large samples its frequency distribution is approximately normal. Values of  $A$  larger than 1 indicate aggregation, less than 1 regularity.

Pielou (1959, 1960, 1961) developed two distance methods to measure pattern. The first uses a sample of distances from randomly located points to the nearest plant and an independent estimate of plant density. From these a statistic,  $\alpha_p$ , can be calculated as follows:

$$\alpha_p = \pi(D)\omega_p$$

where  $D$  is the density of the plants,  $\omega_p$  is the mean squared point-to-plant distance, and  $\pi$  is the trigonometric constant.

The second method (Pielou 1960) uses a sample of distances from randomly chosen plants to their nearest neighbors. A statistic  $\alpha_i$  is calculated in the same way as  $\alpha_p$ , substituting the mean squared plant-to-plant distance for the mean squared point-to-point distance. Pielou (1959) provides tables of confidence intervals and significance levels for values of  $\alpha_i$  and shows how they may be used to interpret  $\alpha_p$  (Pielou 1960).

We mapped the location of each *Pinus edulis* and *Juniperus osteosperma* 10 cm tall or taller in parts of stands A and B. The mapped area in stand A was 2250 m<sup>2</sup>; in stand B it was 2500 m<sup>2</sup>. We checked the accuracy of the maps by comparing plant-to-plant distances calculated from map coordinates to the same distances measured in the field. The greatest difference was about 10 cm.

We classified plants into three height-classes. Small plants were 10 cm to 1 m tall, medium plants between 1 m and 3 m tall, and tall plants were taller than 3 m. The tallest trees in our stands were about 5 m tall. Small plants were not mapped in about one-third of stand A.

For each *P. edulis* in these stands we measured one canopy diameter in an arbitrary direction and estimated the area of its canopy as if it were circular. The living canopies of *J. osteosperma* were often interrupted by

dead branches. We measured the living portions of their canopies and summed the areas estimated from these. Basal areas were calculated for both species from stem diameters measured at ground level. For multi-stemmed plants, the basal areas of all living stems were summed.

We measured the dispersion patterns of the plants on these maps, using both quadrat and distance methods. Small plants were sampled with quadrats 2.5 m on a side (in map scale), medium and tall plants with quadrats 5 m on a side. Quadrats were placed at the intersections of a regular grid of lines 5 scale-meters apart; thus every point on the map was included in exactly one quadrat of a given size. There were 100 large and 400 small quadrats in stand B. Stand A was more irregular, encompassing 90 large and 230 small quadrats.

The spatial dispersions of each size class and species were measured separately and pooled. That is, the null hypothesis of random spatial dispersion was tested by five indices for small *P. edulis*, small *J. osteosperma*, all small plants, medium *P. edulis*, medium *J. osteosperma*, all medium plants, tall *P. edulis*, tall *J. osteosperma*, all tall plants, medium and tall *P. edulis* combined, medium and tall *J. osteosperma* combined, and all medium and tall plants combined.

We constructed Dirichlet domains (Honda 1978, Jack 1967, Mead 1971, Mithen, Harper, and Weiner 1984) for the plants by drawing lines connecting each plant to its immediate neighbors, and then constructing perpendicular bisectors of these lines (Fig. 1). Note that we did not weight the distance from a plant to the bisector by the size of the plant, and thus there is no necessary correlation between the size of a plant and the size of its Dirichlet domain. We estimated the areas of the Dirichlet domains by cutting the polygons from the maps and weighing them. We regressed the areas of the Dirichlet domains on the basal areas, and separately on the canopy areas, of their plants. Regressions on basal areas were compared to regressions on canopy areas, with and without logarithmic transformation, by graphical analysis of residuals.

In stands C and D we located every *P. edulis* and *J. osteosperma* 10 cm or more in height within a square 50 m on a side, noting whether it had become established under a plant canopy or in the open, based on observations of each

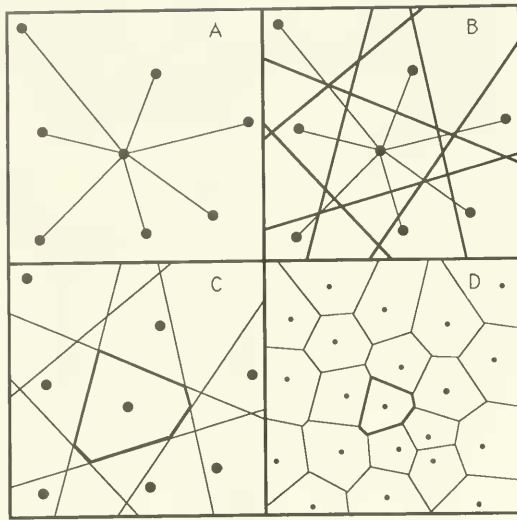


Fig. 1. Construction of Dirichlet domains.

- Draw line segments connecting a focal plant to its neighbors.
- Draw the perpendicular bisector of each line segment.
- The Dirichlet domain is the region closer to the focal plant than all the perpendicular bisectors.
- Repeat for each plant. The Dirichlet domain of each plant is the region closer to it than to any other plant.

tree's association with living or dead shrubs. We measured total plant cover of all species with two 50-m line intercepts. The association of *P. edulis* and *J. osteosperma* with plant cover was tested by a chi-squared test. We did not map these stands but measured distances between neighboring trees in the field. We used Pielou's alpha, to describe the spatial dispersion of the two tree species.

TABLE 1. Stand censuses, divided by height categories ( $10\text{ cm} \leq \text{small} < 1\text{ m} \leq \text{medium} < 3\text{ m} \leq \text{tall}$ ) and by species. In parentheses are numbers per hectare.

		Small plants	Medium plants	Tall plants	Total
Stand A	<i>Pinus edulis</i>	61 (432)	56 (229)	67 (274)	184 (753)
	<i>Juniperus osteosperma</i>	26 (184)	12 (49)	39 (160)	77 (315)
Stand B	<i>P. edulis</i>	88 (352)	32 (128)	11 (44)	131 (524)
	<i>J. osteosperma</i>	86 (344)	9 (36)	41 (164)	136 (544)
Stand C	<i>P. edulis</i>	56 (224)	22 (88)	1 (4)	79 (316)
	<i>J. osteosperma</i>	7 (28)	7 (28)	0	14 (56)
Stand D	<i>P. edulis</i>	47 (188)	30 (120)	4 (16)	81 (324)
	<i>J. osteosperma</i>	34 (136)	46 (184)	17 (68)	97 (388)

## RESULTS

Table 1 shows the number of *P. edulis* and *J. osteosperma* in each stand and the corresponding numbers per hectare. Table 2 shows the five dispersion indices for the trees in stands A and B, and Table 3 the interpretations of these values. In the woodland stands (A and B) small plants tend to be clumped, and larger plants tend to be randomly or uniformly dispersed. The sequence from clumped to random to uniform is violated in only three instances (asterisks in Table 3). These violations may be the result of chance, since the tests for significance were all set at the 5% level and some spurious results are expected among such a large number of separate tests.

All log-log transformed regressions of Dirichlet domain areas on plant canopy areas and basal areas in stands A and B are significant at the 5% level, except for that of *J. osteosperma* in stand A (Table 4, Fig. 2). These regressions show that, on average, larger plants have larger Dirichlet domains and are correspondingly farther from their neighbors. The Dirichlet domains of small plants are more variable in area than those of larger plants. Logarithmic transformation of both variates improves the distribution of variates and residuals and produces reasonable conformity with the assumptions of regression, but it does not change the significance of the regressions. These results are similar to those of regressing the distance between a pair of neighboring plants on the sum of their sizes (Welden 1984, Welden, Slauson, and Ward 1988, cf. Fuentes and Gutierrez 1981, Gutierrez and Fuentes 1979, Nobel 1981, Phillips and MacMahon 1981, Pielou 1960,

TABLE 2. Values of dispersion indices in stands A and B. Indices are identified in the text and these values are interpreted in Table 4. A dash indicates that the test could not be performed.

Stand	Distance methods						Quadrat methods			
	alpha <sub>p</sub>		alpha <sub>i</sub>		A		chi <sup>2</sup>		var/mean	
	A	B	A	B	A	B	A	B	A	B
<i>P. edulis</i>										
Small	0.93	1.04	1.12	0.84	0.83	1.21	12.2	25.0	1.27	1.98
Medium	0.98	1.23	1.15	0.66	0.85	1.83	5.97	—	1.72	1.60
Medium and tall	1.00	0.74	1.04	0.97	0.96	1.38	2.90	2.16	1.48	1.28
Tall	0.84	0.38	0.88	0.91	0.95	0.42	0.17	—	1.10	0.89
<i>J. osteosperma</i>										
Small	1.03	1.36	1.04	1.07	0.99	1.27	—	29.4	1.52	1.15
Medium	0.61	1.06	0.84	0.64	0.72	1.65	—	—	1.04	0.86
Medium and tall	0.73	0.93	1.09	1.29	0.78	0.73	0.24	2.12	0.96	0.86
Tall	0.73	0.73	1.18	1.39	0.75	0.54	0.24	1.10	0.97	0.82
Species combined										
Small	1.25	1.29	0.79	0.86	1.58	1.50	18.1	8.18	1.62	1.65
Medium	1.17	1.58	0.96	0.54	1.22	2.94	2.28	10.9	1.44	2.22
Medium and tall	1.06	0.86	0.94	1.14	1.12	0.92	4.35	0.91	1.34	1.19
Tall	0.92	0.74	0.98	1.13	0.78	0.59	0.60	3.76	1.04	0.95

TABLE 3. Pattern analyses of stands A and B. C indicates that the plants are clumped, R that they are randomly dispersed, U that they are uniformly dispersed. All indicated nonrandom dispersions are significant at the 5% level. A dash indicates that the test could not be performed. Asterisks denote contradictions to the general trend of C - R - U with increasing plant size.

Stand	Distance methods						Quadrat methods			
	alpha <sub>p</sub>		alpha <sub>i</sub>		A		chi <sup>2</sup>		var/mean	
	A	B	A	B	A	B	A	B	A	B
<i>P. edulis</i>										
Small	R	R	R	R*	R	R*	C	C	C	C
Medium	R	R	R	C	R	C	C	—	C	C
Medium and tall	R	U	R	R	R	R	R	R	C	R
Tall	R	U	R	R	R	R	R	—	R	R
<i>J. osteosperma</i>										
Small	R	C	R	R	R	R	—	C	C	C
Medium	U	R	R	R	R	R	—	—	R	C
Medium and tall	U	R	R	R	R	R	R	R	R	R
Tall	U	U	R	U	R	U	R	R	R	R
Species combined										
Small	C	C	R	R*	R	C	C	C	C	C
Medium	R	C	R	C	R	C	R	C	C	C
Medium and tall	R	R	R	R	R	R	R	R	C	R
Tall	R	U	R	R	R	U	R	R	R	R

1961, Yeaton and Cody 1976, and Yeaton, Travis, and Gilinsky 1977).

Plant cover (primarily of *Artemisia*) in stand C was approximately 20%, and about 96% of the *P. edulis* and about 71% of the *J. osteosperma* had become established under plant canopy. Plant cover in stand D was about 18%, and about 93% of the *P. edulis* and about 87% of the *J. osteosperma* had become established under plant canopy. The probability that establishment of *P. edulis* or *J. osteo-*

*sperma* is random with respect to plant cover is less than .001 in every case. The pattern statistic alpha<sub>i</sub> (Pielou 1960) showed no significant deviations from random dispersion among *P. edulis* or *J. osteosperma* in stands C and D.

#### DISCUSSION

Pielou (1959) and Goodall and West (1979) show that distance methods are more sensitive to uniformity and quadrat methods are

TABLE 4. Coefficients of log-log transformed regressions of Dirichlet domain area on canopy and basal areas. Significance is the probability of such data if the true slope and  $r$  equal zero.

Species	Stand	$n$	$r^2$	Y-intercept	Slope	Significance
<i>P. edulis</i>						
Independent variable						
ln (canopy area)	A	98	0.056	10.12	0.13	0.019
ln (basal area)			0.052	11.05	0.11	0.024
ln (canopy area)	B	33	0.272	5.15	0.26	0.002
ln (basal area)			0.191	6.81	0.21	0.011
<i>J. osteosperma</i>						
ln (canopy area)	A	27	0.031	12.50	-0.06	0.377
ln (basal area)			0.020	12.04	-0.04	0.479
ln (canopy area)	B	31	0.367	5.41	0.23	0.000
ln (basal area)			0.352	6.84	0.18	0.000
Species combined						
ln (canopy area)	A	125	0.039	10.49	0.10	0.027
ln (basal area)			0.047	11.15	0.09	0.015
ln (canopy area)	B	64	0.333	5.27	0.25	0.000
ln (basal area)			0.268	6.88	0.18	0.000

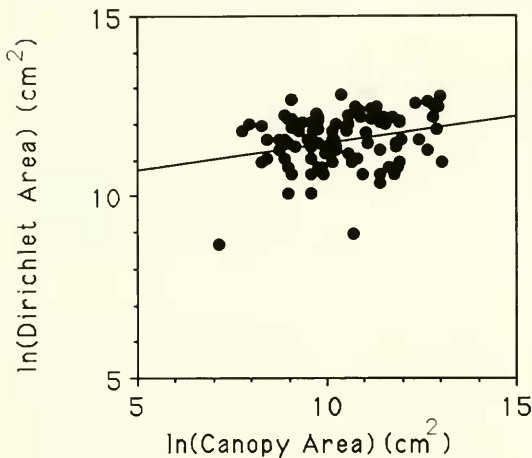


Fig. 2. Regression of Dirichlet domain area on canopy area of piñons in stand A. Both variates have been transformed to their natural logarithms.

more sensitive to clumping. This is borne out by Table 4, where it can be seen that the quadrat methods never detected uniform dispersion while the distance methods did. The distance methods, on the other hand, failed to detect clumping in several cases where it was detected by the quadrat methods.

The trees in the woodland stands (A and B) appear to be interfering (*sensu* Harper 1961, 1977) with one another, either by competition or by allelopathy. The trend from clumped to random to uniform dispersion with increasing plant size suggests density-dependent mortality. Density-independent mortality in a clumped population might con-

ceivably reduce sample sizes in successively larger size-classes until the clumping is no longer detectably different from a random dispersion, but it seems unlikely that it could produce a uniform dispersion (Phillips and MacMahon 1981).

The significant regressions of Dirichlet domain area on plant size indicate density-dependent mortality or density-dependent suppression of growth, or both. We envision two processes leading to this result. First, plants that become established farther from preexisting neighbors become larger because they have access to more unexploited (or unsequestered) resources. Second, established plants prevent the establishment of new neighbors nearby, or impede their growth, because they have exploited (or sequestered) most of the resources in their neighborhoods.

Mithen, Harper, and Weiner (1984) found significant positive relationships between Dirichlet domain area and plant dry weight in even-aged greenhouse populations of *Lapsana communis* L. Although the conditions of their experiments are different (particularly since their plants germinated synchronously), their interpretations of their results are similar to ours here.

Pielou's (1959, 1960) method did not detect any deviation from random spatial arrangement in stands C and D. However, both tree species are significantly associated with plant cover. We presume that these trees became established after long-distance dispersal (> 100 m) from nearby woodlands. The

significant interaction in these stands is evidently not interference between neighboring trees, but amelioration of abiotic stress under the canopies of preexisting plants. Fowells (1965) reports that *P. edulis* requires shade early in its development.

Our evidence for these interpretations is circumstantial. However, given the long lives and slow growth of these plants, and the varying physical environment of the study area, such evidence may be the most informative. These pattern methods integrate the effects of environment and biotic interactions over the life spans of the plants, a time scale not usually accessible to more mechanistic methods.

All our inferences of processes leading to the present pattern require further examination. Although *J. osteosperma* has been reported to produce allelochemicals (Jameson 1971), experiments should be done to determine whether allelopathic effects occur under the conditions and in the soils of the Piceance Basin, and more field studies are needed to determine whether establishment occurs more often near neighbors or far from them. The dynamic behavior of the various pattern indices and regressions should be explored under conditions of density-dependent and density-independent mortality.

#### LITERATURE CITED

- CLAPHAM, A. R. 1936. Over-dispersion in grassland communities and the use of statistical methods in plant ecology. *Journal of Ecology* 24: 232-251.
- FOWELLS, H. A., ED. 1965. *Silvics of forest trees of the United States*. Agriculture Handbook 271. 1965.
- FUENTES, E. R., AND J. R. GUTIERREZ. 1981. Intra- and interspecific competition between matorral shrubs. *Oecologia Plantarum* 16: 283-289.
- GOODALL, D. W., AND N. E. WEST. 1979. A comparison of techniques for assessing dispersion patterns. *Vegetatio* 40: 15-27.
- GOODRICH, S., AND E. NEESE. 1986. Uinta Basin flora. United States Department of Agriculture Forest Service—Intermountain Region. Ogden, Utah.
- GUTIERREZ, J. R., AND E. R. FUENTES. 1979. Evidence for intraspecific competition in the *Acacia caven* (Leguminosae) savanna of Chile. *Oecologia Plantarum* 14: 151-158.
- HARPER, J. L. 1961. Approaches to the study of plant competition. Pages 1-39 in *Mechanisms in biological competition*. Academic Press, New York.
- . 1977. *Population biology of plants*. Academic Press, New York.
- HONDA, H. 1978. Description of cellular patterns by Dirichlet domains: the two-dimensional case. *Journal of Theoretical Biology* 72: 523-543.
- HOPKINS, B. 1954. A new method for determining the type of distribution of plant individuals. *Annals of Botany (London)* 18: 213-227.
- JACK, W. H. 1967. Single tree sampling in even-aged plantations for survey and experimentation. Proceedings, 14th I.U.F.R.O. Congress, Section 25, Munich.
- JAMESON, D. A. 1971. Degradation and accumulation of inhibitory substances from *Juniperus osteosperma* (Torr.) Little. Pages 121-127 in *Biochemical interactions among plants*. National Academy of Science.
- MEAD, R. 1971. Models for interplant competition in irregularly distributed populations. Pages 13-32 in G. P. Patil, E. C. Pielou, and W. E. Waters, eds., *Statistical ecology*, Vol. 2, Sampling and modeling biological populations and population dynamics. Pennsylvania State University Press, University Park.
- MITIEN, R., J. L. HARPER, AND J. WEINER. 1984. Growth and mortality of individual plants as a function of "available area." *Oecologia* 62: 57-60.
- NOBEL, P. S. 1981. Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida*. *Journal of Ecology* 69: 735-742.
- PHILLIPS, D. L., AND J. A. MCMAHON. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69: 97-115.
- PIELOU, E. C. 1959. The use of point-to-plant distances in the study of pattern in plant populations. *Journal of Ecology* 47: 607-613.
- . 1960. A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology* 48: 575-584.
- . 1961. Segregation and symmetry in two-species populations as studied by nearest-neighbour relationships. *Journal of Ecology* 49: 255-269.
- TIEDEMAN, J. A., AND C. TERWILLIGER, JR. 1978. A phytodaphic classification of the Piceance Basin. *Colorado State University Range Science Department Science Series* 31, 265 pp.
- WELDEN, C. W. 1984. Stress and competition among trees and shrubs of the Piceance Basin, Colorado. Unpublished dissertation, Colorado State University, Fort Collins.
- WELDEN, C. W., W. L. SLAUSON, AND R. T. WARD. 1988. Competition and abiotic stress among trees and shrubs in northwest Colorado. *Ecology* 69: 1566-1577.
- WYMORE, I. F. 1974. Estimated average annual water balance of Piceance and Yellow Creek watersheds. Colorado State University Environmental Resources Center Technical Report Series No. 2.
- YEATON, R. I., AND M. L. CODY. 1976. Competition and spacing in plant communities: the northern Mohave Desert. *Journal of Ecology* 64: 689-696.
- YEATON, R. I., J. TRAVIS, AND E. GILINSKY. 1977. Competition and spacing in plant communities: the Arizona upland association. *Journal of Ecology* 65: 587-595.

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